

7. Growth in the two upper and one lower ambulacra of helicoplacoids almost certainly occurred at the distal tips as in other early echinoderms with recumbent ambulacra.
8. Only two body regions have been identified in the helicoplacoid theca, axial ambulacra and perforate extraxial interambulacral pleats. No imperforate extraxial plating has been identified and this body region may have been eliminated during evolution of the helically spiralled body.
9. If helicoplacoids are derived, either a gradual series of morphologic changes produced this unusual new helically spiralled morphology in helicoplacoids from a domal or pyrgate, pentamer edrioasteroid, or a single drastic change in body form triggered the remaining changes to gradually improve functioning of a newly developed helically pleated animal.

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REFERENCES

- Bottjer DJ, Hagadorn JW, Dornbos SQ. 2000.** The Cambrian substrate revolution. *GSA Today* **10**(3): 1–7.
- David B, Lefebvre B, Mooi R, Parsley R. 2000.** Are homolozoans echinoderms? An answer from the axial-extraxial theory. *Paleobiology* **26**: 529–555.
- Derstler K. 1981.** Morphological diversity of Early Cambrian echinoderms. In *Short Papers for the Second International Symposium on the Cambrian System*, Taylor ME (ed.). US Geological Survey Open-File Report 81–743: 71–75.
- Derstler K. 1985.** *Studies on the Morphologic Evolution of Echinoderms*. PhD thesis, University of California, Davis.
- Domínguez-Alonso P. 1999.** The early evolution of echinoderms: the Class Ctenocystoidea and its closest relatives revisited. In *Echinoderm Research 1998: Proceedings of the Fifth European Conference on Echinoderms, Milan/Italy*, Candia Carnevali MD, Bonasoro F (eds). Balkema: Rotterdam; 263–268.
- Dornbos SQ, Bottjer DJ. 2000.** Evolutionary paleoecology of the earliest echinoderms: helicoplacoids and the Cambrian substrate revolution. *Geology* **28**: 839–842.
- Dornbos SQ, Bottjer DJ. 2001.** Taphonomic and environmental distribution of helicoplacoid echinoderms. *Palaios* **16**: 197–204.
- Durham JW. 1966.** *Camptostroma*, an Early Cambrian supposed scyphozoan, referable to Echinodermata. *Journal of Paleontology* **40**: 1216–1220.
- Durham JW. 1967.** Notes on the Helicoplacoidea and early echinoderms. *Journal of Paleontology* **41**: 97–102.
- Durham JW. 1978.** A Lower Cambrian eocrinoid. *Journal of Paleontology* **52**: 195–199.
- Durham JW. 1993.** Observations on the Early Cambrian helicoplacoid echinoderms. *Journal of Paleontology* **67**: 590–604.
- Durham JW, Caster KE. 1963.** Helicoplacoidea: a new class of echinoderms. *Science* **140**: 820–822.
- Durham JW, Caster KE. 1966.** Helicoplacoids. In *Treatise on Invertebrate Paleontology, Part U, Echinodermata 3(1)*, Moore RC (ed.). Geological Society of America and University of Kansas Press: New York and Lawrence; U131–U136.
- Mooi R, David B. 1998.** Evolution within a bizarre phylum: homologies of the first echinoderms. *American Zoologist* **38**: 965–974.
- Mooi R, David B, Marchand D. 1994.** Echinoderm skeletal homologies: classical morphology meets modern phylogenetics. In *Echinoderms Through Time: Proceedings of the Eighth International Echinoderm Conference, Dijon, 6th–10th September, 1993*, David B, Guille A, Feral J-P, Roux M (eds). Balkema: Rotterdam; 87–95.
- Paul CRC. 1977.** Evolution of primitive echinoderms. In *Patterns of Evolution as Illustrated by the Fossil Record*, Hallam A (ed.). Elsevier: Amsterdam; 123–158.

- Paul CRC, Smith AB. 1984.** The early radiation and phylogeny of echinoderms. *Biological Reviews* **59**: 443–481.
- Smith AB. 1986.** Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids. *Palaeontology* **28** (for 1985): 715–756.
- Smith AB. 1988.** Fossil evidence for the relationships of extant echinoderm classes and their times of divergence. In *Echinoderm Phylogeny and Evolutionary Biology*, Paul CRC, Smith AB (eds). Clarendon Press: Oxford; 85–101.
- Smith AB, Jell PA. 1990.** Cambrian edrioasteroids from Australia and the origin of starfishes. *Memoirs of the Queensland Museum* **28**: 715–778.
- Sprinkle J. 1973.** *Tripatocrinus*, a new hybocrinid crinoid based on disarticulated plates from the Antelope Valley Limestone of Nevada and California. *Journal of Paleontology* **47**: 861–882.
- Sprinkle J. 1980.** An overview of the fossil record. In *Echinoderms, Notes for a Short Course*, Broadhead TW, Waters JA (eds). University of Tennessee Department of Geological Sciences, Studies in Geology 3: 15–26.
- Sprinkle J. 1992.** Radiation of Echinodermata. In *Origin and Early Evolution of the Metazoa*, Lipps JH, Signor PW (eds). Plenum: New York; 375–398.
- Sprinkle J, Guensburg TE. 2001.** Growing a stalked echinoderm within the Extraxial-Axial Theory. In *Echinoderms 2000: Proceedings of the Tenth International Echinoderm Conference, Dunedin, New Zealand*, Barker M (ed). Balkema: Lisse; 59–65.
- Sumrall CD. 1994.** Thecal designs in isorophinid edrioasteroids. *Lethaia*, **26** (for 1993): 289–302.
- Sumrall CD. 1996.** *A Phylogenetic Analysis of Echinodermata Based on Primitive Fossil Taxa*. PhD thesis, University of Texas at Austin.
- Sumrall CD. 2000.** Developmental role in echinoderm ambulacral reduction. *Geological Society of America Abstracts with Programs* **32**(7): A-72.
- Ubaghs G. 1971.** Diversité et spécialisation des plus anciens échinodermes que l'on connaisse. *Biological Reviews* **46**: 157–200.
- Ubaghs G. 1978.** Skeletal morphology of fossil crinoids. In *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2(1)*, Moore RC, Teichert C (eds). Geological Society of America and University of Kansas: Boulder and Lawrence; T58–T216.
- Wilbur BC. 2003.** Resolving a growth series within helicoplacoids: implications for functional morphology and systematics. *Geological Society of America Abstracts with Programs* **35**(6): 162.